

Growth, Size Rank, and Maturation of the Freshwater Prawn, *Macrobrachium rosenbergii*: Analysis of Marked Prawns in an Experimental Population

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Abstract. For four months we marked and followed through female maturation and adult male morphotypic differentiation, the growth of all 150 individuals in an experimental population of Malaysian giant freshwater prawns (*Macrobrachium rosenbergii*). Small immature female prawns had high growth rates. Growth of female prawns nearly ceased after maturation. This compensatory growth process produces adult females having a unimodal, symmetrical size distribution with a mean above the size threshold for maturation (about 18–26 g). The small male morphotype has a low growth rate, while the orange claw male morphotype has a high growth rate. As the orange claw males transform to the blue claw morphotype, growth ceases. Examination of changes in size rank during the maturation process supported the leapfrog phenomenon. The fastest growing, largest orange claw male is the first to metamorphose to the blue claw morphotype (at a size of 35 g). As other orange claw males exceed this size, they transform in a sequential process so that the most recent blue claw male is generally the largest blue claw male in the population. Thus, growth of males is compensatory throughout the process of morphotypic differentiation, leading to a wide size range of orange and blue claw males. The leapfrog phenomenon is discussed in terms of the reproductive success of the blue claw males and compared with related growth processes in male poeciliid fishes. Implications of this growth process for aquacultural pro-

ductivity includes the stimulatory effect on the remaining prawns of selectively harvesting the largest blue claw and orange claw prawns and suggests that the inclusion of a small proportion of large “target” blue claw males might stimulate the rapid growth of orange claw males in a population of smaller prawns.

Introduction

Growth of individuals within a population is often highly variable. The causes vary, involving genetic, social, and environmental factors. Because body size often affects reproductive output and survivorship, variation in growth is a very important component of individual fitness. How intraspecific interactions cause variation in growth will be crucial to the evaluation of life history tactics. Variation in growth of aquatic animals is also of practical interest, as it influences the harvest of fisheries and aquaculture systems.

The giant freshwater prawn, *Macrobrachium rosenbergii*, is particularly interesting with respect to variation in growth and the role of size in the social structure of populations. Starting with a cohort of postlarvae having a normal size distribution (Sandifer and Smith, 1975; Ra'anán and Cohen, 1984), growth of juvenile prawns is compensatory (Malecha, 1980), the variance increasing more rapidly than mean size (Ricker, 1975). About half of the population grows rapidly and variably, while the other half grows slowly and relatively uniformly, leading to a markedly, positively skewed size distribution (Wickins, 1972; Forster and Beard, 1974; Ra'anán, 1983; Ra'anán and Cohen, 1985). Both sexes have similar size frequency distributions in populations of immature prawns (Ra'anán and Cohen, 1985). As the individuals mature, the size distribution becomes quite different for males and females. Mature females grow more slowly than males of similar size, and the size distribution of the fe-

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males regains an approximately normal pattern (Cohen *et al.*, 1981). For the males, the skewed distribution is extended, even reinforced, upon maturation (Fujimura and Okamoto, 1972; Smith *et al.*, 1978; Brody *et al.*, 1980; Malecha *et al.*, 1984), and this is associated with the differentiation of three anatomically, physiologically, and behaviorally distinctive adult male morphotypes (Ra'anán, 1982; Ra'anán and Cohen, 1985; Ra'anán and Sagi, 1985; Kuris *et al.*, 1987; Sagi and Ra'anán, 1988; Sagi *et al.*, 1988). Small males include about 50% of the adult males and have small claws, grow slowly, and exhibit a normal size distribution. Orange claw males have relatively larger claws, grow rapidly, are highly variable in size, and include about 40% of the adult males. The remaining 10% are blue claw males. These are also highly variable in size, but grow slowly if at all. Blue claw males are behaviorally dominant over the other morphotypes, and orange claw males are dominant over the small males. Dominance is expressed in several ways, including retreat of subordinate males in the presence of a dominant male. An individual prawn may proceed from a small male to an orange claw and then to a blue claw male in a developmental sequence (Ra'anán and Cohen, 1985; Ra'anán and Sagi, 1985; Kuris *et al.*, 1987, Barki, 1989).

Blue claw males sequester females prior to mating, guard the females, and place spermatophores close to the female genital opening. Small males engage in "sneak" reproductive tactics, attempting to attach spermatophores in the vicinity of the vertical surface of the abdomen of females protected by blue claw males. The orange claw males do not show appropriate reproductive behavior, although they have mature sperm and can achieve mating when isolated with receptive females in aquaria (Ra'anán and Sagi, 1985). Karplus *et al.* (1986) have shown that the proportion of male morphotypes varies significantly with density. At densities as low as 1 prawn/m², the proportion of blue claw males may rise to 20%, while the proportion of small males decreases to 33%. Variable growth and differing reproductive tactics associated with morphologically distinctive types of males have also been recognized in many species of fishes (Parker, 1970; Moav and Wohlfarth, 1974; Gross and Charnov, 1980; Dominey, 1980; Warner, 1984; Gross, 1985), insects (Alcock *et al.*, 1977; Cade, 1981; Thornhill, 1981; Ward, 1983), and crustaceans (Shuster, 1987).

Ra'anán and Cohen (1985) proposed that the first male to attain blue claw status was one of the most rapidly growing orange claw males and that it would be subsequently surpassed by other orange claw males in a "leap-frogging" process such that the most recently metamorphosed blue claw male would generally be the largest blue claw male in the population. To test this hypothesis, we followed the growth of marked individuals in a population, paying close attention to their rank in size and their

morphotypic status as operationally defined in Kuris *et al.* (1987).

The marking procedure also enabled us to define the relationship between growth rate and maturation of the female prawns. Little attention has been paid to growth of female prawns. Although individual juvenile female prawns show variation in size and growth rates comparable to juvenile male prawns, the adult female population has a normal size distribution with a small mean size. Tracking the growth of marked females enabled us to determine how such a size structure resulted during the process of maturation. Finally, we formulated a model for the relationship between growth, maturation, and morphotypic status of both male and female *Macrobrachium rosenbergii*.

Materials and Methods

Source of the animals

Juvenile prawns, averaging (\pm SD) 10.83 \pm 8.55 g were selected haphazardly from a larger prawn population of the same age in a secondary nursery pond operated at the Nir David fish farm. The nursing period was 4 months. An experimental population of 150 individuals was established in a large, 4500-liter tank. All individuals were sexed and weighed. This population was composed of 80 males (average weight \pm SD 10.6 \pm 9.9 g) and 70 females (average weight \pm SD 11.1 \pm 6.1 g). All juveniles were individually marked by tattooing their uropods with a mounted insect pin, according to a method developed originally for crabs by Kuris (1971), and later successfully adapted to prawns (Kuris *et al.*, 1987).

Management procedures

The tank was connected to a biological filter in a closed recirculating system in a prawn hatchery at Ein Hamifratz. Water temperature was regulated between 26–28°C by a thermostat. Substrate, in the form of horizontal hanging nets composed of three layers of three-square-meters each, was provided to increase the submerged surface area and shelter subordinate and newly molted individuals. Prawns were fed once a day with ground fresh fish fillet, supplemented with carp pellets (25% protein). Food was offered in excess, and leftover food particles were removed daily by siphoning the tank bottom. The observation period was 142 days.

Routine measurements

Every two weeks, all prawns were removed from the tank, sexed, and individually weighed. The tattoo identification mark was renewed whenever necessary (mainly following ecdysis).

Females were classified into one of four groups. These were (a) pre-reproductive females, with narrow brood

chambers and no visible gonads; and (b) ripening females, with narrow brood chambers but having visible gonads (Sagi and Ra'anán, 1985). These first groups were immature as males never placed spermatophores upon them. Mature females were either (c) ovigerous with enlarged brood chambers bearing eggs or (d) post-ovigerous, with enlarged brood chambers but no visible gonads. Thus, the appearance of an enlarged brood chamber operationally defined the onset of maturation.

Males were classified according to their morphotypic stage within the male social system (Ra'anán and Cohen, 1985; Kuris *et al.*, 1987).

Statistical analysis

Analysis of male growth characteristics. For each male, body weight was plotted over time. Males were separated into three categories: (1) individuals that were initially SM and remained in this morphotype until the end of the observation period; (2) SM individuals that transformed to the OC morphotype during the observation period; and (3) individuals, which were initially OC males, that transformed to the BC morphotype. On each sampling date, mean weight, standard deviation (SD), and the coefficient of variation, PCV, were calculated for each group of males. As the size distribution was skewed, the median body weights for each of these groups of males on each date were used to generate growth curves.

Daily growth rates (\pm standard error of the mean) were described using the instantaneous rate of growth (also called specific growth rate or relative growth rate), G , where $G = 100(\ln W_t - \ln W_0)/t$, with W_0 and W_t being, respectively, the weights recorded initially and after t days (Fisher, 1946; Ricker, 1975; Kaufmann, 1981). This permitted the comparison of growth rates at different body sizes. The variance of the growth curve parameters was estimated for each morphotype according to Kaufmann (1981). The regression of G on $\ln W$ was calculated for each of the morphotypes, using simple linear regression analysis (Weisberg, 1980). In the case of the OC male category, it was concluded, after assessing the sensitivity of the regression analysis to outlying observations according to Cook and Weisberg (1982), that two (of the 67) observations were outliers. These were excluded from further analysis. The correlations between G and $\ln W$ for the different morphotypes were compared using the Zeller-Theil-Gupta statistic (Ali and Silver, 1985).

The relative size ranking of each individual within the male population was determined by scaling the total weight range at each measurement as 99, attributing to each male a rank according to its relative position between the smallest individual (1) and the largest (100). To examine whether individuals of a particular morphotype tended to gain or lose in relative rank within the male population, we plotted initial rank *versus* terminal rank

of each individual while maintaining the same morphotypic characteristics. The direction of the changes in rank of all individuals within a given morphotype were evaluated using the sign test (Pratt and Gibbons, 1981).

Analysis of female growth characteristics. For each female, body weight was plotted over time. Females were grouped into two categories (immature and mature) and mean weights and PCV were calculated as for males. For each category, the median body weights at different times were used to generate growth curves. Individual growth rate was measured using G . The variance of growth rate and the linear relationship between G and $\ln W$ for each female category were established following similar routines described for analysis of the males.

Results

Evaluation of male growth characteristics

Median growth curves. Figure 1 shows growth curves obtained by plotting the medians of the $\ln W$ distributions of individual males for each morphotype against time. For the SM morphotype, growth rate was low compared with growth rates of animals that transformed to the OC morphotype. Following transformation to the BC morphotype, growth ceased, as reflected in the plateau in the growth curve after 12 weeks. Examination of individual growth curves revealed the same general pattern, although transformation from one morphotype to another occurred at different times (*i.e.*, different individuals spent different lengths of time in each morphotype). The growth rate during the OC phase (as measured by the slope of the growth curve) always remained higher than the growth

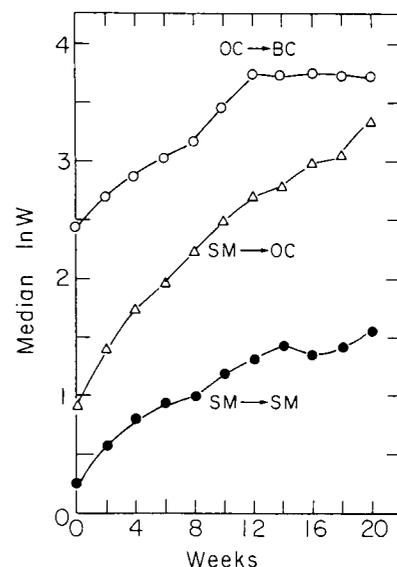


Figure 1. Median growth curves of small males (SM → SM), SM animals that transformed to OC males (SM → OC), and OC animals that transformed to BC males (OC → BC).

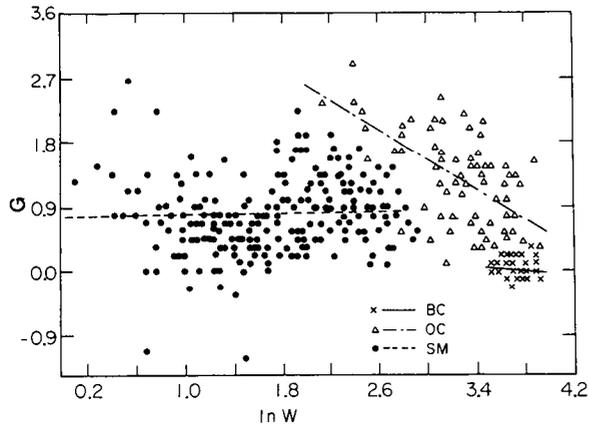


Figure 2. Scatter plots and regression lines for the association of instantaneous growth rate (G) and the natural logarithm of body weight ($\ln W$) of individuals of the three male morphotypes.

rates of the same individual in either SM or BC morphotypic phases.

An examination of the male size distribution within the three morphotypic categories, over the entire observation period, revealed that the weight range of SM males was between 1–15 g (average weight 6.5 ± 4.0 g, PCV = 61.5%), that the weight range of OC males was 10–50 g (average weight 31.2 ± 7.9 g, PCV = 25.3%), while the weight range of BC males was relatively narrow, 35–50 g (average weight 45.0 ± 3.4 g, PCV = 7.5%). The smaller BC males were individuals that were the first to transform into the BC category.

Relationships between growth rate and morphotypic status. The OC males showed the highest growth rate ($G = 1.22 \pm 0.4$), while the BC males had the lowest growth rate ($G = 0.07 \pm 0.09$). Growth effectively ceased when a male transformed into the BC morphotype. The SM males had an intermediate growth rate ($G = 0.83 \pm 0.33$), indicating that this morphotype has a relatively slow growth rate compared to the OC morphotype. Differences in mean G -value between the three male morphotypes were significant (t-test, $P < .001$).

We examined the relationship between G and $\ln W$ for each morphotype (Fig. 2). The growth rate of males in the OC morphotype decreased with increase in $\ln W$ (t-test for significance of slope, two-tailed $P < .001$), while the growth rates of BC and SM males were relatively constant over size. When growth rates of SM and OC males were compared within the range where their $\ln W$ overlapped ($2 < \ln W < 3$), the OC males had a significantly higher G (95% confidence band for the difference between the mean G of OC and SM males with the same $\ln W$ values). There was also a narrow overlap in the weight range of BC and OC males ($3.5 < \ln W < 3.8$), where G -values of the OC males were significantly higher than those of the BC males (t-test, two-tailed $P < .05$).

Relationship between size rank and morphotype. Figure 3 describes the relationship between the initial size rank of an individual, when first categorized into a specific morphotype, and its terminal ranking determined at the last measurement before its transformation into the next morphotype. All points that are located on the Initial rank = Terminal rank line represent individuals that did not change their size rank during the time they were in a particular morphotype. All points below the line represent a loss in rank, while those located above the line represent a gain in rank. The rank of all BC males decreased with time (sign-test, 1-tailed $P < .0005$) while ranks of all OC males increased (sign test, 1-tailed $P < .0003$). As for the SM males, 17 individuals lost in rank, while 28 individuals gained. There was a tendency to gain in rank while in the SM developmental stage, but this was not significant (sign test, 2-tailed $P = .072$).

Evaluation of female growth characteristics

Growth curve of M. rosenbergii females. Figure 4 shows a growth curve of the medians of the $\ln W$ distributions of individual females (both immature and mature). Prior to sexual maturation, females grew exponentially, as demonstrated by the linear increase of $\ln W$. After sexual maturation, growth ceased. A comparison of individual growth curves of females revealed a similar pattern, although growth rate prior to sexual maturation, and the time of maturation, varied.

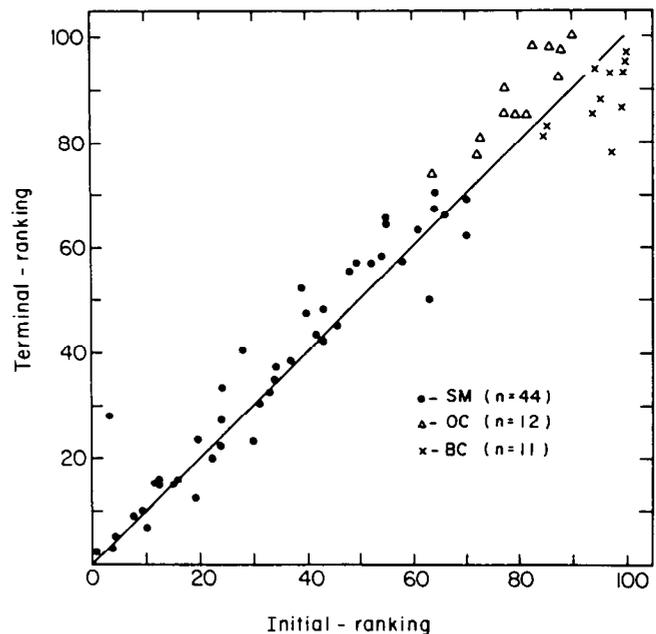


Figure 3. The relationship between initial and terminal size rank for the different morphotypes. Each point represents the rank of an individual when it entered the indicated morphotype (initial) and when it was last recorded in that morphotype (terminal). The diagonal line represents growth with no change in rank. Points above this line represent individuals that gained in rank when they were in a particular morphotype.

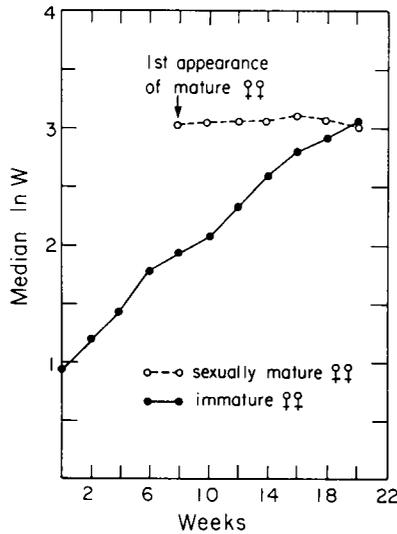


Figure 4. Median growth curves of females before and after sexual maturation.

A comparison of the size distribution of females before and after maturation revealed that the weight range of immature females was relatively wide, from 0.5 to 24.8 g ($W = 6.12 \pm 5.0$ g, $PCV = 81.7\%$), while that of the sexually mature females was relatively narrow, from 15.2 to 27.2 g ($W = 21.35 \pm 3.22$ g, $PCV = 15.1\%$). Part of the variation in weight of the sexually mature females may be attributed to the presence of eggs on ovigerous females. This comprised 10–15% of their weight (Ra'anán, pers. obs.). For the entire female population, it is notable that parallel to the increase in average weight with time, there was a continuous decrease in the coefficient of variation.

Relationship between female growth rate and sexual maturation. Figure 5 presents the relationship between G and $\ln W$ for all females that matured ($n = 24$), and all females that remained immature throughout the experiment ($n = 24$). Growth rate was inversely proportional to weight for all females. However, comparing animals of similar body weight, G -values for growth during the immature phase of females that ultimately matured were usually higher than those calculated for females that did not mature. G -values for females after becoming sexually mature were lowest, $0.2 \pm .12$, indicating that growth effectively ceased at maturation.

Relationship between female age, size, and initiation of maturation. Of 48 females, 24 became sexually mature during the observation period. The females began to mature between the sixth and eighth week (Fig. 6A). For the remainder of the period, a relatively constant proportion (range 9–21%) matured per two-week interval.

At maturity, ovigerous females exhibited an approximately normal weight distribution (Fig. 6B, $W = 21.12 \pm 5.20$ g, $PVC = 24.6\%$). The age of females when first ovigerous was negatively correlated with initial body

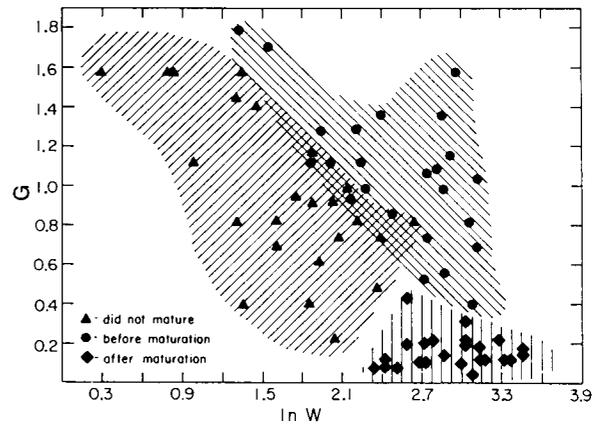


Figure 5. The relationship between female instantaneous growth rate (G) and the natural logarithm of body weight ($\ln W$). Triangles represent growth of females that were immature throughout the experiment. Circles represent growth of females prior to maturation for females that did mature during the experiment. Diamonds represent growth of females after maturation.

weight (Fig. 7, $r = -.712$, $P < .002$). The females that were initially larger matured earlier than the smaller ones.

The largest females at stocking usually remained the largest throughout the experiment, whether they matured or not (Fig. 8). Further, while both immature and mature females spanned a similar initial weight range, the weight of mature females was both higher and less variable than that of the immature females.

Discussion

These results confirm (Ra'anán and Cohen, 1985; Kuris *et al.*, 1987) that small males grow slowly, that orange claw males grow rapidly, and that blue claw males molt infrequently, if they molt at all. Regression analysis in-

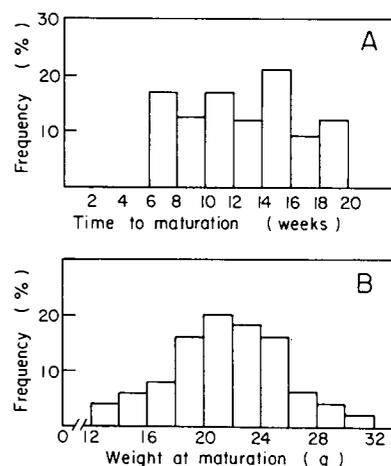


Figure 6. (A) Frequency distribution for the age (in weeks) at onset of maturation of females. (B) Frequency distribution of female body weight at onset of maturation.

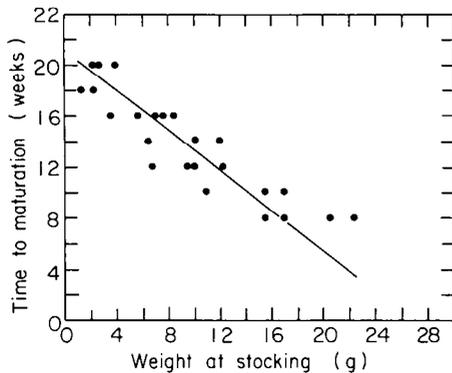


Figure 7. The correlation between age at maturation of females and their initial weight recorded at stocking.

indicated that growth rate of small males did not vary with size (Fig. 2). Thus, absolute size did not affect the relative size rank of these males throughout the observation period (Fig. 3). The significant tendency for small males to gain in rank is accounted for by the particularly poor growth performance of a few individuals. The high G for the smaller orange claw males indicates that the size disparity between small males and orange claw males increases with time, furthering the differentiation between these morphotypes. As the orange claw males increase in size and approach their metamorphosis to the blue claw morphotype (Kuris *et al.*, 1987), growth rate slows. Perhaps this decreased growth of the largest orange claw males is an energetic cost of morphotypic differentiation.

Ra'anán and Cohen (1985) observed that the size of blue claw males in a population was inversely proportional to the amount of algae adhering to their cuticles. Because coverage by epibionts is an indicator of time since the previous ecdysis (Smith *et al.*, 1979), this led to the hypothesis that the larger blue claw males were the more recently metamorphosed. Hence, Ra'anán and Cohen (1985) proposed the leapfrog hypothesis that orange claw males continue to grow and transform to the blue claw morphotype when they exceed the largest blue claw males in the population. Our size rank analysis provides direct support for the leapfrog growth phenomenon and permits a more explicit description of this unusual, socially mediated growth pattern.

Generally, the most rapidly growing, largest orange claw male becomes the first male to metamorphose into a blue claw male (Fig. 9). Other rapidly growing orange claw males soon exceed this first blue claw male and become the new, larger, blue claw males. Consistent with this model, the orange claw and blue claw males exhibit a similar range in sizes, and the largest male in pond populations may be either a blue claw or an orange claw male. The leapfrog growth pattern is probably due to social interactions among males, because males isolated in small cages did not follow this pattern (Karplus *et al.*, 1991).

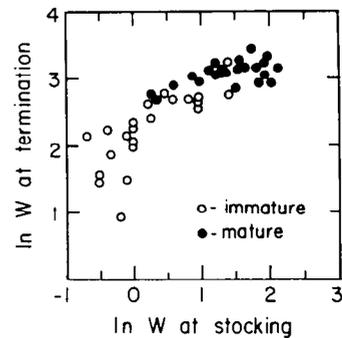


Figure 8. The relationship between weight of females at stocking and upon termination of the observation period.

A few orange claw males transformed to the blue claw morphotype while still somewhat smaller than the largest previous blue claw male. This variability may be due to variation in the time lag from the commitment to transform in molt stage D_1 (when new cuticular details are differentiated, Drach, 1939) to the time of ecdysis. If a male that committed early was slow to molt, it could be exceeded in size by a prawn that committed at a later time, but which passed through the proecdysial process more rapidly.

Recently, Barki (1989) showed that the largest blue claw male in a mixed population of blue claw and orange claw males is dominant over all orange claw and the smaller blue claw males. This dominance provides the α -male advantageous access to resources. Larger males presumably acquire larger or better territories and are more likely to sequester reproductive females for mating (Ra'anán and Cohen, 1985). Thus, the reproductive success of the early transforming, smaller, blue claw males probably declines over time as larger blue claw males enter the population.

The leapfrog model for male morphotypic differentiation is superficially similar to maturation of certain male poeciliid fishes (Borowsky, 1973a, b; 1987; Sohn, 1977; Campton and Gall, 1988). In small groups, the first

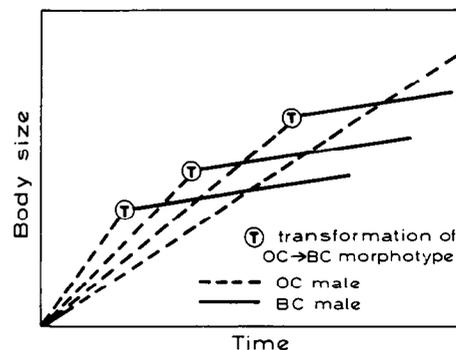


Figure 9. A model for the relationship between maturation and growth in males.

male fish to mature is usually the smallest. Males that mature later do so at larger sizes. In fishes this pattern is socially mediated. But the size variation exhibited by these male fishes is much less than that of *M. rosenbergii*, and in some experimental and natural circumstances, males frequently matured when smaller than other males in the population (Borowsky, 1978b, 1987). Behavioral dominance is associated with adult male size for *Xiphophorus maculatus* (Borowsky, 1973b) but not for *Girardinus metallicus* (Farr, 1980). In contrast, the presence of blue claw males suppresses neither growth nor metamorphosis of orange claw males [although the presence of either blue claw or orange claw males suppresses the growth but not the maturation of the small males (Ra'an and Cohen, 1985)]. Experiments with poeciliid fishes have usually been conducted with a paired or small group (*e.g.*, 4) experimental design; thus the consistent replacement based on size rank that distinguishes the leapfrog model has not yet been shown in these fishes. The socially mediated leapfrog model of male morphotypic differentiation is a highly distinctive growth and maturation phenomenon, perhaps unique to *M. rosenbergii* and related prawns that may have a similar morphotypic system (Kuris *et al.*, 1987).

The growth rate of immature females was relatively high; approaching that of orange claw males (compare Fig. 1, 2 with 4, 5). After maturation, growth slowed considerably but did not cease (Fig. 5). Variation in size decreased with time because growth rate declined markedly with increasing size whether the prawns matured or not (Fig. 5). Thus, a model for female growth (Fig. 10) is quite different from the model for male growth (Fig. 9). The initially highly variable female size distribution [indistinguishable from juvenile males (Ra'an and Cohen, 1984)] is ultimately replaced by a relatively normal distribution. Such a growth pattern is seen in many aquatic organisms (Ricker, 1975). Early in life there is compensatory growth; presumably because, among postlarvae, a size advantage, even though small in absolute terms, leads to a feeding advantage that exaggerates the size disparity in the population (Borowsky, 1978a). Later growth becomes compensatory because smaller animals have a higher growth rate, and growth slows as maturation approaches. Females then accumulate in a relatively narrow size range once they cross the size threshold (more realistically a size range) at which they mature (Fig. 10). The existence of the size threshold is the mechanism that produces a normal size distribution of adult females.

These findings have potential application to prawn aquaculture. Monosex growth experiments using females should yield a more homogenous product. Selective harvest of large blue and orange claw males is clearly beneficial as the growth rate of the remaining male prawns will increase due to the leapfrog mechanism. Population experiments with a small proportion of large blue claw

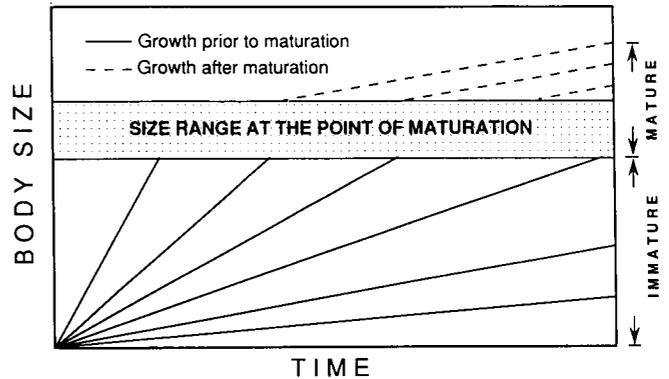


Figure 10. A model for the relationship between maturation and growth in females. The shaded size range is the normally distributed size at maturation (see Fig. 6A).

males should prove interesting. The presence of such males might provide a “target” for rapid growth of orange claw males by preventing metamorphosis to the blue claw morphotype at sizes below that of the target males.

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